

TUARANGISAURUS AUSTRALIS SP. NOV. (PLESIOSAURIA: ELASMOSAURIDAE)
FROM THE LOWER CRETACEOUS OF NORTHEASTERN QUEENSLAND, WITH
ADDITIONAL NOTES ON THE PHYLOGENY OF THE ELASMOSAURIDAE

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The skull and associate cervical vertebrae of an elasmosaur from the Lower Cretaceous of northeastern Queensland are described as a new species of *Tuarangisaurus*, *Tuarangisaurus australis*. They represent the oldest record of that genus and the first secure outside New Zealand. A phylogenetic analysis based on 19 characters of the skull and cervical vertebrae is undertaken. One tree is presented, including all valid members of the Elasmosauridae for which sufficient cranial material is known. The results give an example for the interrelationship of the Elasmosauridae and show the probable position of *Tuarangisaurus*. □ *Plesiosauria, Elasmosauridae, Tuarangisaurus, Lower Cretaceous, Albian, Queensland.*

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The plesiosaurian Elasmosauridae is known from the Lower Jurassic to the Upper Cretaceous, during which time it had an almost worldwide distribution. Most taxa referred to this group had an extremely elongated neck and a proportionately small head.

In Australia, only a small number of elasmosaur remains are known (Cruickshank et al., 1999; Kear, 2003). Among them, there are 4 rather complete specimens, of which 2 are represented by about 80% of the postcranium. The first of these has been excavated by a field-party of the Queensland Museum at the Walsh River (Doncaster Member, Wallumbilla Formation, Late Aptian) west of Chillagoe (NE Queensland); the second one was found at Grampien Valley (Doncaster Member, Wallumbilla Formation, Late Aptian) near Richmond (N Queensland) (Sachs, 2004).

Another specimen from Andamooka in the South Australian Museum, Adelaide is about 50-60% complete and consists of opalised bones (Kear, pers. com. 2001).

The fourth more complete specimen is the holotype of *Woolungasaurus glendowerensis* Persson (1960). The type material was discovered in 1891 (QMF3567) and 1893 (QMF3568) at Glendower Station near Hughenden and has been restudied (Sachs, 2004). Another specimen Persson (1982) referred to *Woolungasaurus* is a skull that is broken into an anterior and posterior part. The posterior portion was discovered first (by T. Noonan) along with a number of vertebrae and

was donated to the Geological Survey of Queensland (GSQF10552, F10550 a+b and F10551). Later, in 1976, a field party comprising R. Molnar, R. Thulborn and M. Wade discovered the anterior part of the skull. This specimen was first catalogued at the Australian Museum in Sydney (old catalogue number AM F60056), but has since been transferred to Brisbane where both parts were donated to the Queensland Museum.

Other probable elasmosaur remains were found in the Northern Territory (Bathurst Island Formation, Albian, sensu Murray 1987) and in Western Australia (Colalura Sandstone, Bajocian, sensu Cruickshank & Long, 1998 and Molecap Greensand, Cenomanian-?Santonian, sensu Teichert & Matheson, 1944).

A greater number of elasmosaur specimens, including relatively complete skeletons, are known from New Zealand (Hector, 1874; Hiller et al, 1997; Owen, 1861, 1870; Seeley, 1877; Welles & Gregg, 1971; Wiffen & Moislcy, 1986). On the basis of this material *Mauiasaurus haasti* Hector, 1874 and *Tuarangisaurus keyesi* Wiffen & Moislcy, 1986 were erected. In general the remains from New Zealand are younger than the Australian ones. *Mauiasaurus* is known from the Conway Formation (Maastrichtian), while *Tuarangisaurus* are from the Tahora Formation (Mid-Campanian).

In this paper the skull described by Persson (1982) shall be redescribed and classified. Based on this specimen and its associated postcranial elements, 19 phylogenetically interesting features

are proposed. An analysis of these characters within the Elasmosauridae and *Muraenosaurus* as outgroup member was undertaken.

ABBREVIATIONS. *Institutional Abbreviations.* AM, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; GPIM, Geologisch-Paläontologisches Museum, Münster; GSQ, Geological Survey of Queensland, Brisbane; MLP, Museo de La Plata, La Plata; NZGS, New Zealand Geological Survey, Lower Hutt; QM, Queensland Museum, Brisbane; UCMP, University of California Museum of Paleontology, Berkeley; USNM, United States National Museum of Natural History, Washington D.C.

Anatomical Abbreviations. aae, atlas-axis-complex; aar, angular-articular complex; aas, angular-articular suture; an, angular; bo, basioccipital; bm, bite mark; d, dentary; en, external naris; exo, exoccipital; fr, frontal; gf, glenoid fossa; hy, hyoid; ipf, interpterygoid fenestra; j, jugal; mt, mandibular tooth; mx, maxilla; mxp, maxillary process; mxt, maxillary tooth; ns, neural spine; pa, parietal; pb, parietal bridge; pl, palatine; pm, premaxilla; pmr, premaxillary ridge; pmt, premaxillary tooth; po, postorbital; prf, prefrontal; ps, parasphenoid; pt, pterygoid; rp, retroarticular process; q, quadrate; qe, quadrate condyle; sa, surangular-articular; sq, squamosal.

SYSTEMATICS

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA De Blainville, 1835

Superfamily PLESIOSAUROIDEA Nopesa, 1928

Family ELASMOSAURIDAE Cope, 1868

Tuarangisaurus Wiffen & Moisley, 1986

TYPE SPECIES. *Tuarangisaurus keyesi* Wiffen & Moisley, 1986.

DIAGNOSIS. See Wiffen & Moisley (1986: 207).

Tuarangisaurus australis sp. nov.

Woolungasaurus cf. *W. glendowerensis* Persson, 1982: 647-655.

"*Woolungasaurus*" Thulborn & Turner, 1993: 489ff.

Elasmosaurid: Kear, 2003: 288f.

ETYMOLOGY. Latin *australis*, southern; refers to the southern continent Australia.

MATERIAL. Holotype, QMF11050, an almost complete, but crushed skull and mandible, with attached atlas-axis complex; QMF12216-19, an anterior cervical vertebra; QMF12217, 2 associated posterior cervical vertebrae.

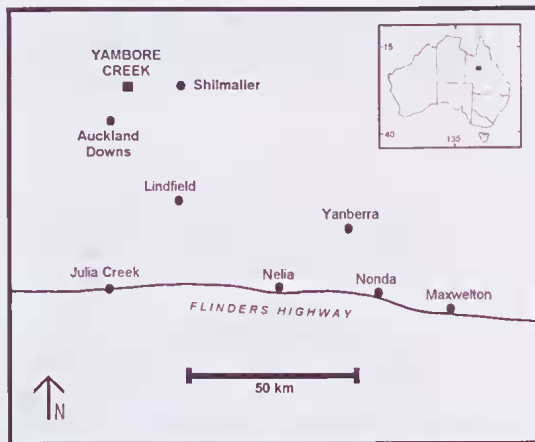


FIG. 1. Map of the wider Julia Creek area, showing the locality of QMF11050 at Yambore Creek.

TYPE LOCALITY. (Fig. 1) Yambore Creek, N of Julia Creek, N Queensland, Toolebuc Formation, Wilgunya Group, Albanian (Senior et al., 1978).

DIAGNOSIS. Premaxillae forming narrow dorsal keel along midline bearing 5 teeth each; last premaxillary tooth at premaxillary-maxillary suture; posterior maxillary process following jugal over entire length and terminating at the level of last dentary tooth; jugal long, low; anterior margin of dentary forming a beak; mandibular symphysis short, expanded to level of dentary tooth four; dentary with 18 teeth per ramus; last dentary teeth more prominent than last maxillary teeth; retroarticular process short relative to jaw length; atlas-axis-complex short and high, ventrally bearing prominent sagittal crest; anterior cervical vertebrae shorter than high.

DESCRIPTION. As mentioned before, the skull consists of two pieces, and is broken just anterior of the orbita. It is almost complete, but compressed dorsolaterally, so that only the left side is well-preserved (Figs 2, 3, 6). Parts of the skull, such as the skull roof and the occipital region could not be described properly as the specimen is badly crushed. The anterior portion of the skull, as well as most of the right mandibular ramus and the dentition is well visible. As is usual in elasmosaurs the skull is relatively long and low. The external naris is visible as a broad oval opening that is situated close to the orbita. The latter is prominently developed and, due to the lack of the ventral border by the maxilla, nearly circular in shape. About in the middle of the orbita, an elongate

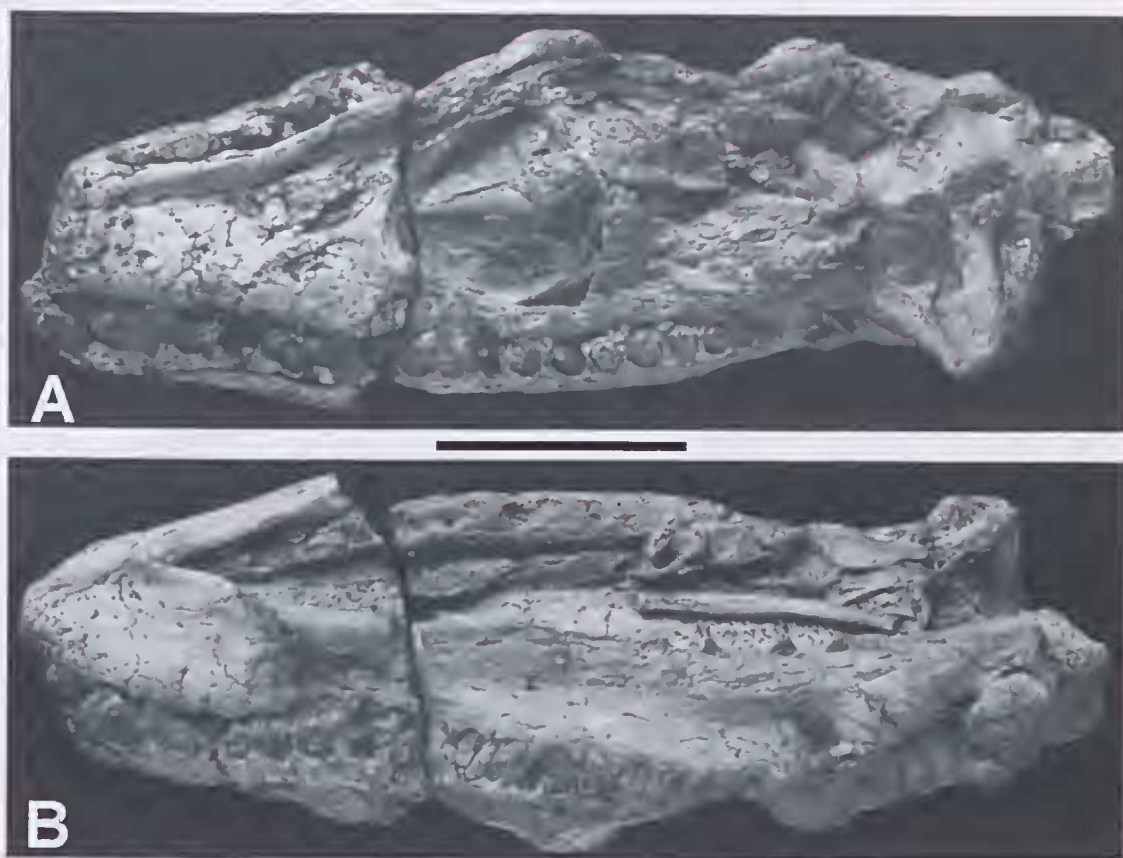


FIG. 2. Skull of *Tuarangisaurus australis* sp. nov., QMF11050 in dorsal (A) and ventral (B) views. Scale = 10cm.

element is visible. Persson (1982) misidentified this bone as the frontals, therefore concluding that the dorsal and the ventral half of the left orbita were the left and the right orbitae. Thulborn & Turner (1993) showed that this structure could be a part of either the pterygoid or the vomer. In the posterior part of the skull, the quadrate and the quadrate condyle are well visible. The right mandibular ramus is almost complete and still articulates with the quadrate. A well preserved hyoid is situated ventrally, in the posterior part of the specimen (Fig. 4). Posteriorly still in articulation with the skull is the atlas-axis complex (Fig. 5A). The fact that the atlas and axis are co-ossified indicates that the specimen represents an adult individual. As the atlas is still in connection with the condylus occipitalis and also partly covered by the squamosal, its shape could not be described. The axis on the other hand, as well as the ventral section of the atlas-axis complex is well visible.

As Thulborn & Turner (1993) showed, there are 3 bite marks of a larger plesiosaur visible on the skull (Fig. 3). A very prominent bite mark is situated in the anterior section of the lower jaw, somewhat behind the symphyseal part on the right ramus. A second relatively large bite mark is situated further posteriorly on the lateral surface of the right mandibular ramus, underneath the coronoid process. The third, relatively small, bite mark is on the left side in the lower part of the squamosal. These bite marks could originate from a large plesiosaur, such as *Kronosaurus queenslandicus*, that has been found in the same area.

Premaxilla. The premaxilla is visible on the left side of the skull and is here almost completely preserved. Only the anteriormost part is eroded and therefore missing. In anterodorsal aspect both premaxillae are well ossified and are separated by a barely visible, straight suture. Ventrally the well-preserved suture to the maxilla runs posteromedially at an angle of about 60° to

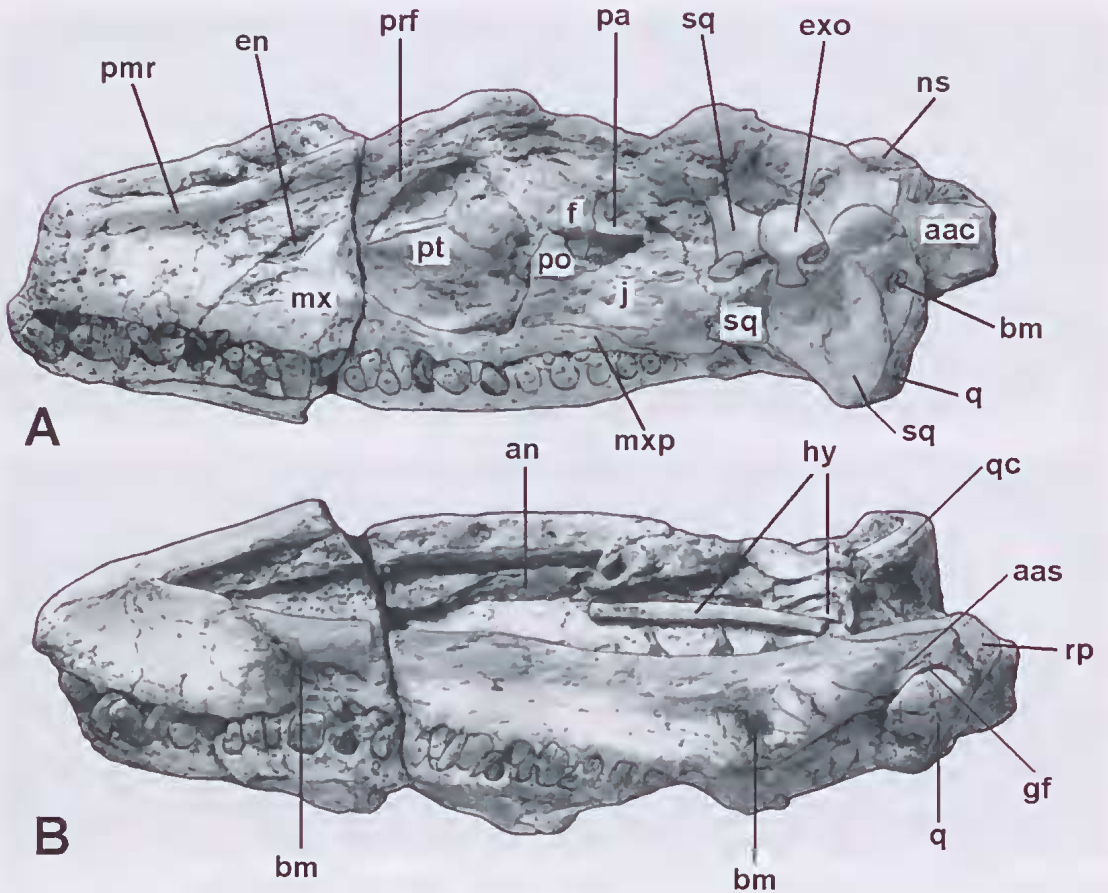


FIG. 3. Skull of *Tuarangisaurus australis* sp. nov. QMF11050 in dorsal (A) and ventral (B) views with explanations.

the transverse plane to the anterolateral edge of the external naris. With a broad dorsal section the premaxilla forms the slightly concave medial edge of the external naris. Behind the external naris, it touches the dorsal margin of the maxilla with a short suture. The posterior termination of the premaxilla, probably to the frontals, is not preserved. The tooth-bearing part is somewhat more robust and bears three teeth. Although the anteriormost section of the premaxillae is missing, it can be calculated that two more teeth were present, bringing the total to five. The first preserved tooth (pmt 3) is relatively short and completely exposed. The next one (pmt 4) is massively developed, but incomplete, as most of the labial and the total apical part are missing. The third preserved tooth (pmt 5) is badly crushed, but was also massively build. It is situated directly at the premaxillary-maxillary suture and is approximately twice as large as the

first preserved maxillary tooth. Between each tooth there is a gap of about 1cm for the interlocking of the dentary teeth.

Maxilla. The left maxilla is almost completely preserved. Only the part that turns posteriorly to frame the orbita anteroventrally and contact the anterior section of the jugal lacks its dorsal margin. On the right side of the skull only the tooth-bearing part of the maxilla is visible. Generally the maxilla is a massive element. It contacts the premaxilla anteroventrally and here forms the lateral and posterior edge of the external naris. With the projection of the dorsal-most part, it contacts a structure that might represent the prefrontal. As mentioned before the posterior section of the maxilla is incompletely preserved. At the posteriormost part that is formed as a long process, an irregular suture to the jugal is visible. It ventrally follows the jugal to nearly its posterior end and thereby gradually

thins out dorsoventrally, terminating immediately behind the level of the last dentary tooth. The tooth-bearing part of the maxilla is somewhat more robust and nearly all teeth are still in their alveoli. The second, third and fourth tooth are very prominent, in which the third maxillary tooth appears to be the largest in the maxilla. The teeth become gradually smaller posteriorly. In the most posterior section two extremely small replacement teeth are situated. In the right maxilla 12 teeth are visible, in the left one 14 (in contrast to Persson (1982: 649) who counted 10 in the right and 11 in the left maxilla), so that probably a total number of 15 or 16 teeth per side was present.

Postorbital. The postorbital section of the specimen is heavily crushed. The only more undistorted fragment is a short triangular shaped piece that is situated in about the middle of the posterior part of the enlarged orbita. It contacts the jugal with a well visible, smooth, ventrally convex suture. This fragment appears to represent only the anterior section of the ventral portion of the postorbital so that the bone was probably more expanded posteriorly. Some other fragments, which are situated underneath the named element and medially of the orbita, could also belong to the postorbital.

Frontal. A broad, flat element that is situated above the named postorbital fragment is here interpreted as part of the frontals. Its visible dorsal surface is smooth and shows a shallow vault in about its midsection. As the underlying parietal fragment bears a sagittal crest, this vaulting can be the result of post-burial compression.

Prefrontal. A low, elongate, slightly curved element that is situated laterally, behind the premaxilla, touching the anterodorsal process of the maxilla, is here interpreted as the prefrontal. It forms most of the dorsal edge of the orbita.

Parietal. Although there are some fragments present in the area of the skull roof where the temporal fenestrae were placed, only one can clearly be determined as part of the parietal. It shows a well developed, sharp, but low crest. On both sides of the crest the dorsal margin is shallowly inclined. This fragment probably formed part of the most antromedial edges of the temporal fenestrae.

Jugal. The jugal is well exposed on the left side and, in lateral view, has a rectangular outline. Its original shape cannot be reconstructed with certain, as part of the anterior section that probably contacted the midsection of maxilla and took part

of the ventral framework of the orbita is not preserved. Posteriorly the jugal contacts the squamosal with a well visible, somewhat anteriorly oriented, serrated suture. Ventrally the irregular posteroventrally running suture between the jugal and maxilla is visible. Dorsally, in the preserved anterior section, the jugal contacts the postorbital with a slightly concave suture.

Squamosal. The squamosal is almost completely preserved on the left side, in which only its dorsal margin is missing. Anteriorly it contacts the jugal with a high, serrated suture. In lateral view the ventral surface of the squamosal is shallowly posteroventrally curved. In ventral view it can be seen that the bone was here relatively thin. Posteriorly the squamosal covers the quadrate laterally and is then, with its posterior margin, slightly up- and forwardly arched. The suture between the squamosal and the quadrate is not visible, indicating that this area was well ossified. A triangular shaped fragment that is situated anterior of the ?exoccipital could be a part of the posterodorsal arch of the squamosal to the parietal.

Quadrate. The quadrate is well visible on the left side and is covered by the squamosal laterally. Due to the compression the quadrate has moved medially, so that its condyle has an anteromedial position. The latter does not seem to be depressed; it has a rectangular shape and is expanded medially with the ventral surface well rounded anteroposteriorly. At the lateral side of the ventral margin a shallow depression is visible. The posterior side of the condyle is somewhat ventrally oriented. Interestingly there is a concave excavation on the internal side of the condyle, so that at its dorsal and ventral side a short tip is formed. This concavity seems not to be produced postmortem. It could have served for the articulation of the quadrate process of the pterygoid. A dividing of the articulation surface in two clearly distinguishable condyles (condylus lateralis quadrati and condylus medialis quadrati, after Maisch, 1998) as it can be find e.g. in *Muraenosaurus*, is not present. At the lateral side the condyle emerges from the prominent shaft of the quadrate in which it is well curved postero-medially. As mentioned before a clear suture between the quadrate and the squamosal cannot be seen. Eventually a line that starts at the lateroventral side of the squamosal-quadrate-complex and is upwardly directed could represent this suture, but similar lines are visible in other parts of the skull too and may be quoted as breaking lines rather than sutures. Dorsally, the thin

quadrate process of the pterygoid, is attach to the condyle.

?Pterygoids. Situated in the middle of the orbita there are 2 elongated, broad fragments, which were interpreted as frontals by Persson (1982). Thulborn & Turner (1993) pointed out that they might represent midline bones of the palate and could be parts of either the vomer or the pterygoids. I agree with this determination. Unfortunately, because of their poor and fragmentary preservation it is impossible to give a clearer statement. Only the position and the visible shape as broadly rounded makes it probable that these elements are parts of the pterygoids.

Braincase Elements. Situated at the level of the upper part of the squamosal, inward of the atlas-axis-complex, there is an isolated element. It consists of a main body that has a nearly quadratic outline and two short, broad processes, which are situated at the end of the main body. The later is relatively flat and has a slightly expanded end, opposite of where the processes are situated. The surface of this portion is shown as deeply convex, but it seems that parts of the margin are broken. The short ?lateral edge that is exposed, bears a crest. The named processes, which are probably incompletely preserved, are shown as short and broad. The upper one of these has a nearly horizontal position in the specimen and is broad oval in cross-section. The lower process is more vertically directed. Its basal margin seems to be tighter than the well-expanded ventral margin. It was not possible to make a secure determination of this element, but it shows similarities to the exoccipital-opisthotic (these bones are often fused in plesiosaurs, as seen e.g. in *Muraenosaurus*, Maisch, 1998, fig. 9, here also called otoccipital).

Dentary. The lateral side of the mandible is completely exposed at the left side of the specimen. The symphysis is straight and relatively short (expanded to the level of the fourth dentary tooth). A suture separating the two rami is not visible, which again shows that the skull was well ossified. The anteriormost part of the dentary is oblique posteroventrally by an angle of about 50° to the vertical plane. Laterally, behind the symphyseal portion the margin is smoothly depressed and bears some small foramina of different sizes. The dorsal side of the dentary is more robust. Towards its midsection the mandibular ramus becomes slightly lower dorsoventrally. Posteriorly, in the coronoid section, the ramus is again high and then inclined

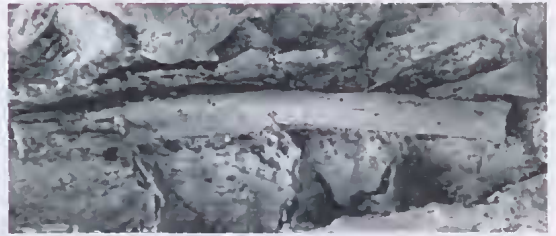


FIG. 4. Hyoid of *Tuarangisaurus australis* sp. nov. QMF11050 in ventral view, measuring 10cm.

posteroventrally towards the glenoid fossa. The ventral margin of the ramus is well rounded and thickened anteriorly. The suture from the dentary to the surangular-articular-complex and the angular is only barely visible, due to the presence of a bite mark (Fig. 3). The dorsal side of the surangular-articular complex bears a sharp edge and slopes down by an angle of about 40° to the horizontal plane. Altogether the mandible bears 36 alveoli (18 per ramus), in which mostly parts of the teeth are still present. Only the anterior-most teeth are prominent, with mandibular teeth 2-5 developed as large fangs.

Angular-Surangular-Articular. The angular is only partially visible. Internally, at the left ramus it is particularly detached, but can only be described as very thin, flat element as no characteristics are present. Better preserved is the posterior part, which is well visible at the right mandibular ramus. The retroarticular process is broken off and somewhat displaced. In lateral view it is short and almost quadratic in shape. It shows a slight transversal concavity at its posterior edge. The suture from the angular to the articular-surangular (according to Brown, 1981, these bones appear to be fused in all plesiosaurs, so that this suture should here only be called angular-articular suture) is well visible in the ventral section of the posterior part of the right ramus. The suture first runs straight posteriorly and is then, at the level of the anterior section of the glenoid fossa upwardly and slightly hindwardly curved, from where it runs straight posteriorly. Its termination is unclear as it is last visible directly underneath the glenoid fossa (the section behind is thus called the angular-articular-complex). The latter is still connected with the quadrate so that its shape cannot be described.

Hyoid. Both hyoids are preserved (Fig. 4) in which only the right one is well exposed, while the left one is underlying the right, so that only its posterior margin is visible. They are rod-shaped,

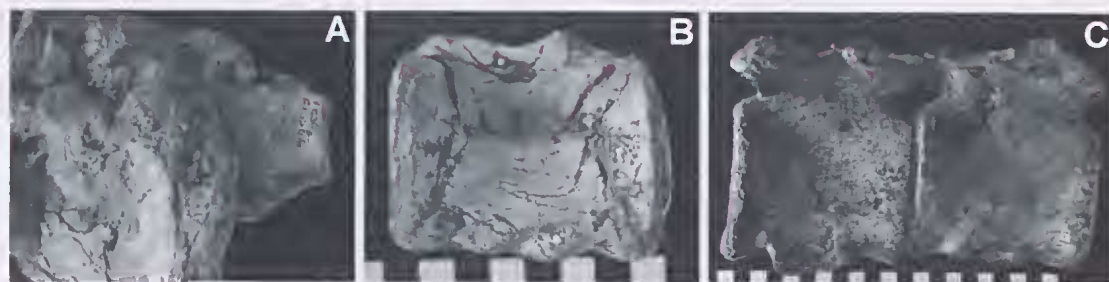


FIG. 5. Vertebrae of *Tuarangisaurus australis* sp. nov. QMF11050 in lateral views. A, atlas-axis complex; B, anterior cervical vertebra; C, posterior cervical vertebrae; scale bar units = 1cm.

very long, slightly curved and slender. The anterior and posterior end facets are oval in cross-section. The anterior end facet is only weakly concave while the posterior one shows a somewhat stronger concavity. Both facets are slightly broader than the shaft. The later is flattened and has a sharp medial edge, while the lateral edge is well rounded. The anterior half of the right hyoid is somewhat depressed dorsoventrally and therefore slightly broadened lateromedially.

Atlas-Axis Complex. The atlas-axis complex is still connected with the skull (Fig. 5A), therefore only the axis is well exposed and can be described. In general the complex has a nearly quadratic shape and is relatively high. In the center of the ventral surface a prominent, sharp sagittal keel is formed. This keel is present upon the entire length of the centrum and anteriorly becomes larger dorsoventrally. Posteriorly the keel is fused with the edge of the articular facet. On both sides of the keel the ventral margin is slightly longitudinally excavated. The rib facets are situated on the lateroventral side of the complex. On the left side also part of the cervical rib is preserved that has a horizontally oval cross-section and is lateromedially relatively thin. The lateral side of the atlas-axis complex is nearly flat and only in the ventral half posteriorly slightly depressed. Dorsally parts of the thin neural arches are preserved. The neural canal was relatively broad, ventrally just weakly concave and occupied about 50% of the breadth of the axis centrum. The articular facet of the latter is about circular and slightly concave. Its dorsal side is almost straight; the lateral sides are weakly rounded. At the ventral side the attachment of the named keel is visible medially.

Dorsally, anterior of the atlas-axis complex, there is a thin, well-rounded crest that is mostly covered by sediment. The posterior margin of

this crest shows a breaking surface. It most probably is this the neural spine that has been pressed forwards during the compaction of the skull.

Cervical Vertebrae. The centrum of the preserved isolated anterior cervical vertebra (QMF12216-19) has a broad oval outline and is about as wide as long, but clearly lower (5B). Its articular facets are weakly concave, with well-rounded edges. The lateral margin is depressed at one side. In about its mid-section a sharp, medially situated lateral longitudinal crest is formed. Dorsally and ventrally of the crest the margin is longitudinally excavated. Due to the compression, the neural canal is not visible. The rib facets are situated laterally, about in the middle of the ventral surface. They are elongated and ovoid in outline. The ventral surface of the centrum is somewhat depressed. A well developed thin sagittal crest is visible that separates two relatively small nutritive foramina, which are situated in the anterior half of the centrum. On both sides of the crest, the margin is depressed anteroposteriorly.

The posterior cervicals (QMF12217) are accurately preserved (Fig. 5C). The centra are slightly broader than long and longer than high, so that they have a nearly quadratic outline. Dorsally and ventrally, the centra are weakly excavated medially. The ventral margin of the centra is concavely depressed. Medially, somewhat anterior to the midline, two relatively large nutritive foramina are present. A small, flat crest separates them. The rib facets are very prominent, elongated oval in outline and are situated ventrally in the middle of the lateral side. Anterior and posterior to the rib facets the lateral margin is somewhat concave. Each rib facet is oriented lateroventrally at an angle of about 45° to the vertical plane. In the second vertebra, remains of the cervical ribs are preserved. Laterally, above the parapophyses a weak

longitudinal crest is visible. This crest probably represents the lateral longitudinal crest that is well developed in the anterior cervical vertebra. Above the crest the lateral margin is somewhat depressed. The articular facets of the centra are weakly concave, with rounded edges. A dorsal suture between the centrum and the neural arches is not visible. The neural arches are relatively thin and border the broadly triangular neural canal. The margin of the zygapophyses is discernable. In lateral view the prezygapophyses rise above the level of the centrum to about half of their length, in which they are dorsally oriented at an angle of about 40° to the horizontal. The postzygapophyses are higher than the level of the prezygapophyses. They do not rise over the level of the centrum and are dorsally oriented at an angle of about 60° to the horizontal plane. The neural process is present only by its basal margin. It is relatively thin, but prominently broadened anteroposteriorly.

COMPARISON OF *TUARANGISAURUS KEYESI* AND *TUARANGISAURUS AUSTRALIS*

The type material of *T. keyesi* Wiffen & Molesley, 1986, comprises a skull (NZGSCD425) (Fig. 7) and the 9 anterior-most cervical vertebrae including the atlas-axis complex (NZGSCD426). The skull is fairly complete and, except for the posterior sections of the mandibulae and the occipital region, well preserved. *T. keyesi* shares a number of characters with *T. australis*. In both the premaxillae form a beak with a narrow dorsal keel along their midline. The posterior sections of the premaxillae form the concave medial edge of the external nares. Each premaxilla bears five fang-like teeth; the last of them is very prominent and situated directly at the premaxillary-maxillary suture. The later runs to the anterolateral margin of the external naris with an angle of about 60° to the horizontal. The maxilla forms the lateral and posterior edge of the external

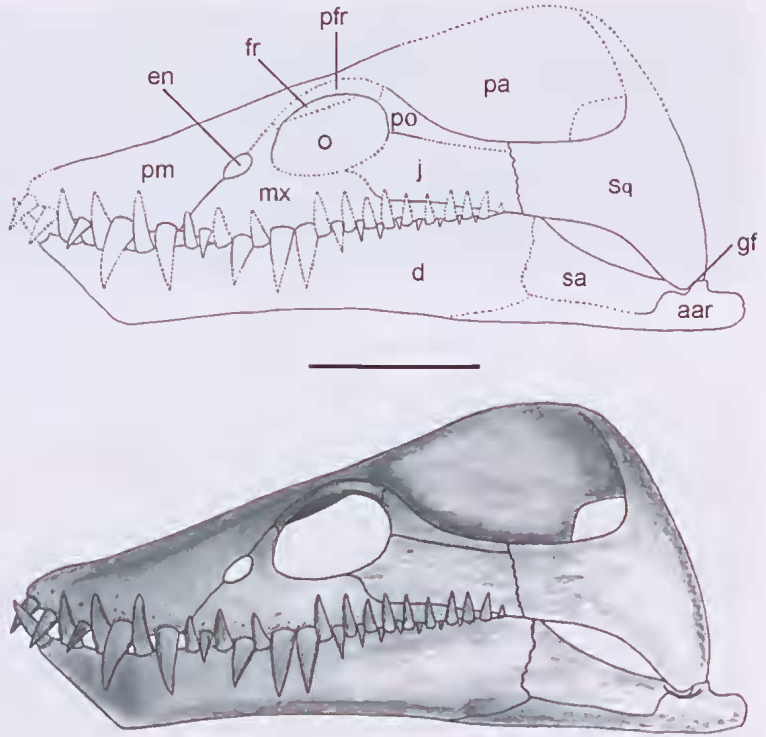


FIG. 6. Reconstruction of the skull of *Tuarangisaurus australis* sp. nov. in lateral view; A, outline drawing (stippled areas are incomplete or not preserved); B, restoration. Scale = 10cm.

nares. Posteriorly a thin maxillary process is formed that follows the jugal to its posterior section, thereby becoming gradually smaller dorsoventrally. The maxillary tooth count is 15-?16 per side. The anterior section of the jugal contacts the maxilla and the postorbital with a large serrated suture. Posteriorly the jugal contacts the squamosal via a distinct serrated suture. The dorsal jugal-postorbital suture is somewhat concave. The ventral surface of the squamosal is shallowly posteroventrally curved. In lateral view the squamosal is only slightly up- and forwardly arched. The anteriormost part of the dentary is posteroventrally oriented by an angle of about 50° to the transverse plane. The anterior portions of the dentary form a beak. The posterior dentary teeth are very prominent and clearly larger than the posterior maxillary teeth. Towards its midsection the dentary becomes slightly narrower dorsoventrally. Posteriorly in the coronoid section, the jaw becomes higher again. The ventral margin of the mandibular ramus is rounded and anteriorly relatively thick. The axis is nearly quadratic in outline, having a

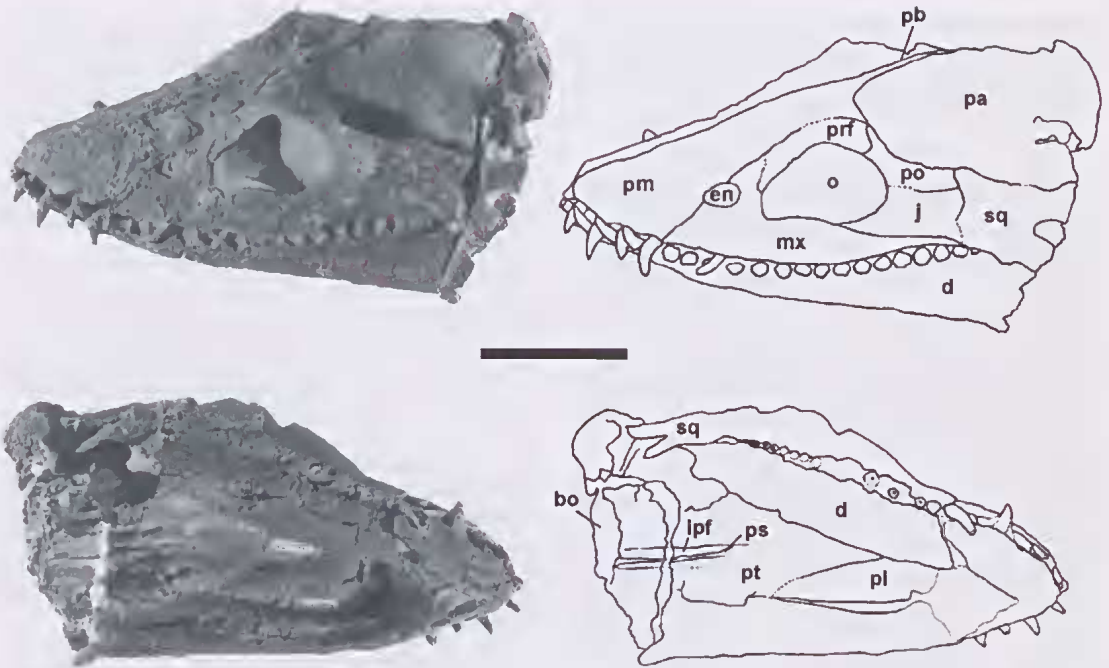


FIG. 7. Skull of *Tuarangisaurus keyesi* NZGS CD425 in lateral and ventral view with schematic outline drawings (stippled areas are incomplete or not preserved). Scale = 10cm.

prominent sagittal keel in the centre of the ventral surface. The cervical rib is lateroventrally directed by an angle of about 45°. The neural canal is relatively broad and occupies about 50% of the breadth of the axis centrum.

T. australis can be distinguished from *T. keyesi* by a number of osteological features, its provenience and age. All materials of *T. keyesi* known so far are from the Mangahouanga Stream site at Hawke's Bay (North Island, New Zealand). The fossil bearing Maungataniwha Member of the Tahora Formation is interpreted as being approximately mid-Campanian in age (Isaac et al., 1991). The Queensland specimen is from the Albian Toolebuc Formation.

The osteological differences between *T. australis* and *T. keyesi* are the position of the external nares, which in *T. keyesi* are somewhat more anteriorly situated, about at the level of the third and fourth maxillary teeth. The third premaxillary tooth that in *T. keyesi* is very large and about as prominent as the 5th premaxillary tooth, while it is rather short in *T. australis*. The last premaxillary tooth that (calculated from the size of the alveoli), in *T. keyesi* did not differ much in size from the 1st maxillary tooth, while in *T. australis* the last premaxillary tooth is about

twice as large as the first maxillary tooth. The posterior process of the maxilla, which in *T. keyesi* terminates at the level of the penultimate dentary tooth, while it terminates directly behind the last dentary tooth in *T. australis*. The anterior parietal section that in *T. keyesi* is formed as a thin bridge, while it is rather sharp in *T. australis*. The jugal, that in *T. keyesi* is rather trapezoid in outline, while it appears to be more rectangular in *T. australis*. The jugal-squamosal suture that in *T. keyesi* is clearly more anteriorly situated than in *T. australis*. The quadrate condyle, which in *T. australis* is shorter and more robust. The mandibular symphysis that in *T. keyesi* only expands to the level of dentary tooth 3, while it expands to the level of dentary tooth 4 in *T. australis*. The dentary that in *T. keyesi* bears 21 teeth per ramus and only 18 in *T. australis*. The dentary teeth, which in *T. keyesi* are almost equal in size throughout the dentition, while in *T. australis* the anterior 5 teeth are larger. The retroarticular process that in *T. keyesi* is about twice as long as broad, while it is about as long as broad in *T. australis*. The posterior articular facet of the axis, which in *T. keyesi* is broad oval in shape and deeply concave, while it is more circular and less concave in *T. australis*.

Based on the listed osteological similarities *T. australis* is referred to *Tuarangisaurus*, and because of the identified differences from *T. keyesi*, it is treated as a separate species.

CLADISTIC ANALYSIS

The ingroup includes all valid members of the Elasmosauridae of which sufficient cranial material is known. Thus *Elasmosaurus*, *Aphrosaurus*, *Fresnosaurus* and *Muraenosaurus* are excluded from the analysis. As outgroup member *Muraenosaurus* was chosen, which according to O'Keefe (2002) belongs to the Cryptoelididae, although it has long been included in the Elasmosauridae. Recent analyses of elasmosaurid taxa have been undertaken by Carpenter (1999), Bardet et al. (1999) and Gasparini et al. (2003), and the characters are partly based upon their results.

REFERRED TAXA. OUTGROUP: *Muraenosaurus* Seeley, 1874. INGROUP: *Occitanosaurus* Bardet, Godefroit & Seiaou, 1999, *Brancaosaurus* Wegner, 1914, *Libonectes*, Carpenter, 1997, *Thalassomedon* Welles, 1943, *Tuarangisaurus* Wiffen & Moislley, 1986, *Callawayasaurus* Carpenter, 1999, *Styxosaurus* Welles, 1943, *Hydralmosaurus* Welles, 1943, *Aristoneustes* Cabrera, 1941, *Hydrotherosaurus* Welles, 1943 and *Terminonatator* Sato, 2003.

CHARACTER DESCRIPTIONS. 1. Orbita - temporal fenestra relative size. 0. equal in size. 1. orbita smaller than temporal fenestra. (modified from Gasparini et al., 2003). Outgroup. In *Muraenosaurus* the orbitae and temporal fenestrae are about equal in size (Andrews, 1910, fig. 46). Ingroup. In most elasmosaurs the temporal fenestrae are clearly larger than the orbitae, as present in *Occitanosaurus* (Bardet et al., 1999, fig. 3), *Libonectes* (Carpenter, 1997, fig. 2), *Thalassomedon* (Carpenter, 1999, fig. 12), *Callawayasaurus* (Carpenter, 1999, fig. 13), *Styxosaurus* (Welles & Bump, 1949, fig. 3), *Hydralmosaurus* (Carpenter, 1999, fig. 7), *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001) and *Tuarangisaurus*. In *Brancaosaurus* both are about equal in size (Wegner, 1914, fig. 1). In *Aristoneustes* (Gasparini et al., 2003) and *Terminonatator* (Sato, 2003) the conditions are unknown.

2. Premaxillary tooth count. 0. five. 1. between 1 and 6. 2. > 6. (modified from Gasparini et al., 2003). Outgroup. Primarily five premaxillary teeth are present in *Muraenosaurus* (Andrews, 1910). Ingroup. The number of premaxillary teeth is highest in *Aristoneustes* with 10-13 per side (Gasparini et al., 2003), which also is the most increased number of premaxillary teeth in all sauropterygians. *Terminonatator* has nine premaxillary teeth per side (Sato, 2003). Eight premaxillary teeth have been estimated for *Elasmosaurus* (Cope, 1869, 1875), but

only 6 alveoli are visible (ANSP 10081, Sachs, pers. obs. 2001). Five premaxillary teeth are present in *Libonectes* (Welles, 1949), *Brancaosaurus* (Wegner, 1914), *Hydralmosaurus* (Carpenter, 1999), *Callawayasaurus* (Welles, 1962), *Styxosaurus* (Welles & Bump, 1949), *Occitanosaurus* (Bardet et al., 1999), *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001, in addition to 4, counted by Welles, 1943) and *Tuarangisaurus*. The number of premaxillary teeth is lowest in *Thalassomedon* with only 4 teeth per side (Welles, 1943).

3. Premaxilla-parietal contact. 0. absent. 1. present. (modified from Carpenter, 1999). Outgroup. In *Muraenosaurus* a premaxillary-parietal contact is not established as the frontals intermediate between the 2 elements (Andrews, 1910). Ingroup. A premaxilla-parietal contact is established in *Callawayasaurus*, *Hydralmosaurus*, *Libonectes*, *Styxosaurus*, *Thalassomedon*, *Tuarangisaurus keyesi* (after Carpenter, 1999: tab. 2) and *Terminonatator* (Sato, 2003). The premaxillae and parietals are separated by the frontals in *Occitanosaurus* (Bardet et al., 1999, fig. 3), *Brancaosaurus* (Wegner, 1914, fig. 1) and *Hydrotherosaurus* (Sachs, pers. obs. 2001). This section of the skull is not well preserved in QMF 11050 and *Aristoneustes* (Gasparini et al., 2003).

4. Maxilla-jugal contact. 0. maxilla does not follow the jugal posteriorly. 1. a posterior process of the maxilla follows the jugal to its posterior section. 2. maxilla terminates posterior of the jugal. Outgroup. In *Muraenosaurus* only the anteriormost sections of the jugals are in touch with the maxillae (Andrews, 1910, fig. 46). Ingroup. In most elasmosaurs the maxilla follows the jugal to nearly its posterior end, as it is present in *Libonectes* (Welles, 1949, plate 1), *Styxosaurus*, *Hydralmosaurus* (Welles, 1952, fig. 5+6) and *Tuarangisaurus*. In *Brancaosaurus* (Wegner, 1914, fig. 1) and *Thalassomedon* (Carpenter, 1999, fig. 13) the maxilla is somewhat larger than the jugal and runs further posteriorly. This appears also to be the case in *Terminonatator* (Sato, 2003, fig. 5a), although the jugal is only fragmentarily preserved. For *Callawayasaurus* Welles (1962: 18) wrote 'the maxillary probably ends posteriorly below the middle of the jugal arch in a downcurved slender point'. Only a short contact in the anterior section of the jugal is present in *Occitanosaurus* (Bardet et al., 1999, fig. 3). The jugal is not known in *Aristoneustes* (Gasparini et al., 2003) and the condition is unclear in *Hydrotherosaurus* as not clear suture is visible in that part of the skull (UCMP33912, Sachs, pers. obs. 2001).

5. Maxillary tooth count. 0. 17 or more. 1. 14-16. 2. 13 or fewer. Outgroup. According to Brown (1981) *Muraenosaurus* bears 16 teeth per maxilla. Ingroup. The number of maxillary teeth is 14-16 in *Libonectes* (14 after Carpenter, 1999) and *Tuarangisaurus* (15-16). The number is lower than 14 in *Hydralmosaurus* (13 after Welles, 1952), *Terminonatator* (13, after Sato, 2003), *Occitanosaurus* (12 after Bardet et al., 1999), *Styxosaurus* (11 after Welles & Bump, 1949) and *Callawayasaurus* (9 after Welles, 1962). 13 alveoli are visible in

Hydrotherosaurus, in which the posterior ones are not clear (UCMP 33912, Sachs pers. obs. 2001). According to Welles (1943: 158) *Thalassomedon* only bears 7 teeth per maxilla, while in the drawing of Carpenter (1999, fig. 12) 13 teeth are visible. The largest number of maxillary teeth among all sauropterygians is present in *Aristonectes* with about 51-53 teeth per side (Gasparini et al., 2003). The number is unclear in *Brancaesaurus*, as the maxillae are incompletely preserved (Wegner, 1914).

6. Maxillary termination. *O.* maxilla terminates posterior to the level of the last dentary tooth. *I.* maxilla terminates close to the level of the last dentary tooth. Outgroup. In *Muraenosaurus* the maxilla terminates farther behind the level of the last dentary tooth about at the level of the posterior margin of the orbita (Andrews, 1910, fig. 46). Ingroup. The maxilla terminates close to the level of the last dentary tooth in *Callawayasaurus* (Welles, 1962, fig. 3), *Styxosaurus* (Welles, 1952, fig. 5), *Terminonator* (Sato, 2003, fig. 5), *Tuarangisaurus* and probably also in *Hydralmosaurus* (Welles, 1952, fig. 6) and *Aristonectes* (Gasparini et al. 2003, fig. 1). The maxilla is further posteriorly expanded in *Libonectes* (Carpenter, 1997, fig. 5), *Thalassomedon* (Carpenter, 1999, fig. 12) and *Brancaesaurus* (Wegner, 1914, fig. 1). The situation is unknown in *Occitanosaurus* as the lower jaw is missing (Bardet et al., 1999) and in *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001) as this part of the skull is not well preserved.

7. Jugal-squamosal contact. *O.* by a short suture or no contact is established. *I.* by a long suture. Outgroup. In *Muraenosaurus* only a short suture in the ventral half of the squamosal is developed (Andrews, 1910, fig. 46). Ingroup. A long squamosal-jugal contact is present in most elasmosaurs. It can be found in *Styxosaurus*, *Hydralmosaurus* (Welles, 1952, fig. 5+6), *Thalassomedon* (Carpenter, 1999, fig. 12), *Libonectes* (Welles, 1949, plate 1) and *Tuarangisaurus*. In *Callawayasaurus* this section is somewhat distorted, but a long suture between the squamosal and the jugal is visible (Welles, 1962, fig. 3). A short suture is developed in *Occitanosaurus* (Bardet et al., 1999, fig. 3) and *Brancaesaurus* (Wegner, 1914, fig. 1) as here the anterior margin of the squamosal also articulates with the postorbital. As mentioned before the jugal is only fragmentarily preserved in *Terminonator* (Sato, 2003) and is missing in *Aristonectes* (Gasparini et al., 2003), so that no statements are possible for these taxa. In *Hydrotherosaurus* the posterior suture to the squamosal is not preserved (UCMP33912, Sachs, pers. obs. 2001).

8. Jugal-postorbital contact. *O.* suture long relative to the length of the jugal. *I.* suture short relative to the length of the jugal. (modified from Bardet et al., 1999). Outgroup. A long postorbital suture is present in *Muraenosaurus*, reaching over most of the dorsal edge of the jugal (Andrews, 1910, fig. 46). Ingroup. The jugal-postorbital suture is comparatively long in *Styxosaurus* (Welles, 1952, fig. 5), *Hydralmosaurus* (Welles, 1952, fig. 6), *Callawayasaurus* (Welles, 1962, fig. 3), *Occitanosaurus* (Bardet et al., 1999, fig. 3), and *Tuarangisaurus*. It is short in *Libonectes* (Welles, 1949, plate 1), *Thalassomedon*

(Carpenter, 1999, fig. 12) and *Brancaesaurus* (Wegner, 1914, fig. 1), while this section of the skull is not preserved in *Aristonectes* (Gasparini et al., 2003) and *Terminonator* (Sato, 2003) and the condition is unclear in *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001).

9. Jugal-orbita contact. *O.* Jugal does not take part in the margin of the orbita. *I.* Jugal takes part in the margin of the orbita. Outgroup. In *Muraenosaurus* the jugal forms the posterior half of the lateral margin of the orbita (Andrews, 1910, fig. 46b). Ingroup. The jugal is participated in forming the orbita in all referred elasmosaur taxa with the exception of *Occitanosaurus* (Bardet et al., 1999, fig. 1) Here the jugal is dorsally covered by the postorbital. In *Terminonator* only a fragment of the right jugal is preserved, but according to its position it appeared to have been participated in forming the orbita too (Sato, 2003, fig. 5). The jugal is unknown in *Aristonectes* (Gasparini et al., 2003).

10. Jugal-temporal fenestra contact. *O.* jugal is excluded from the dorsal margin of the temporal fenestra. *I.* jugal takes part in the dorsal margin of the temporal fenestra. (sensu Carpenter, 1999). Outgroup. In *Muraenosaurus* the jugal is not participated in the margin of the temporal fenestra, as it is dorsally covered by the postorbital, which forms the anteroventral margin of the fenestra (Andrews, 1910). Ingroup. The jugal takes part on the dorsal margin the temporal fenestra in *Thalassomedon* (Carpenter, 1999, fig. 12), *Callawayasaurus* (Welles, 1962, fig. 3), *Hydralmosaurus* (Welles, 1952, fig. 6), *Styxosaurus* (Welles, 1952, fig. 5), *Libonectes* (Carpenter, 1997, fig. 5) and *Tuarangisaurus*. The jugal is dorsally covered by the postorbital and therefore not participated in *Occitanosaurus* (Bardet et al., 1999, fig. 3) and *Brancaesaurus* (Wegner, 1914, fig. 1). The condition is unknown in *Terminonator* (Sato, 2003) and *Aristonectes* (Gasparini, et al. 2003) and unclear in *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001).

11. Postfrontal. *O.* present. *I.* absent. (sensu Bardet et al., 1999). Outgroup. The postfrontals are present in *Muraenosaurus* (Andrews, 1910). Ingroup. The postfrontal is a primitive element and is present in *Occitanosaurus* (Bardet et al., 1999, fig. 3) and *Brancaesaurus* (Wegner, 1914, fig. 1) and absent in all other referred elasmosaur taxa. The according section of the skull is unknown in *Aristonectes* (Gasparini et al., 2003).

12. Squamosal-postorbital contact. *O.* present. *I.* absent. Outgroup. In *Muraenosaurus*, a clear contact between the postorbital and the squamosal is present (Andrews, 1910, fig. 46). Ingroup. The squamosal does not touch the postorbital in *Styxosaurus* (Welles, 1952, fig. 5), *Thalassomedon* (Carpenter, 1999, fig. 12), *Callawayasaurus* (Welles, 1962, fig. 3) and *Tuarangisaurus*. A contact is present in *Occitanosaurus* (Bardet et al., 1999, fig. 3) and *Brancaesaurus* (Wegner, 1914, fig. 1). In *Hydrotherosaurus* a zigzagged suture seems to be present, but is not well visible (UCMP 33912, Sachs, pers. obs. 2001). A contact has also been suggested for *Hydralmosaurus* (Welles, 1952, fig. 6), but this reconstruction appears to be doubtful. The section is not

well preserved in *Libonectes* (Carpenter, 1997, fig. 2) and is missing in *Aristonectes* (Gasparini et al., 2003) and *Terminonator* (Sato, 2003).

13. Dentary teeth per ramus. *0*. 21 or more. *1*. 18–20. *2*. 17 or fewer. Outgroup. In *Muraenosaurus* the tooth count is 22 per dentary ramus (Brown, 1981). Ingroup. The number of dentary teeth is 18–20 in *Libonectes* (17/18, after Carpenter, 1997), *Callawayasaurus* (19, after Welles, 1962), *Terminonator* (17/18, after Sato, 2003) and QMF1150 (18). According to Welles (1943) the mandible of *Thalassamedon* only bears 16 teeth per ramus. However, following the photo of UNSM 50132 in Carpenter (1999, fig. 12) at least 19 teeth per ramus are present. The number is higher in *Tuarangisaurus keyesi* (21, NZGS CD425, Sachs pers. obs. 2001) and *Brancaesaurus* (21, after Wegner, 1914) and lower in *Styxosaurus* (17, after Welles & Bump, 1949). In *Hydralmosaurus* 17 teeth are present (after Welles, 1952), but Carpenter (1999, p. 156) suggests that the number might be higher. The number is most increased in *Aristonectes* with about 60–65 teeth per dentary ramus (Gasparini et al., 2003). The condition is unclear in *Hydrotherosaurus* (UCMP 33912, Sachs, pers. obs. 2001) and unknown in *Occitanosaurus* (Bardet et al., 1999).

14. Shape of dentary teeth. *0*. posterior-most dentary teeth are not markedly more prominent than posterior-most maxillary teeth. *1*. posterior-most dentary teeth very prominent in relation to the posterior-most maxilla teeth. Outgroup. In *Muraenosaurus* the posterior dentary teeth are about equal in size with the last maxillary teeth (Andrews, 1910, fig. 46). Ingroup. The posterior dentary teeth are clearly more prominent than the posterior maxillary teeth in *Libonectes* (Carpenter, 1997, fig. 5), *Styxosaurus* (Welles, 1952, fig. 5), *Hydralmosaurus* (Welles, 1952, fig. 6), *Callawayasaurus* (Welles, 1962, fig. 3), *Terminonator* (Sato, 2003, fig. 5), *Hydrotherosaurus* (UCMP33912, Sachs, pers. obs. 2001) and *Tuarangisaurus*. The posterior dentary teeth are about equal in size with the last maxillary teeth in *Thalassomedon* (Carpenter, 1999, fig. 12). This section is not well preserved in *Brancaesaurus*, but the teeth seem not to be more prominent than the posterior maxillary teeth (GPIM A36, Sachs, pers. obs. 1999). Rather small posterior dentary teeth have been reconstructed for *Aristonectes*, but they still appear to be larger than the posterior maxillary teeth (Gasparini et al., 2003).

15. Length of retroarticular process. *0*. long relative to jaw length. *1*. short relative to jaw length. Outgroup. *Muraenosaurus* has a long retroarticular process (Andrews, 1910, fig. 46). Ingroup. The retroarticular process is comparatively short in *Styxosaurus* (Welles, 1952, fig. 5), *Hydralmosaurus* (Welles, 1952, fig. 6), *Callawayasaurus* (Welles, 1962, fig. 3), *Terminonator* (Sato, 2003, fig. 5), *Aristonectes* (Gasparini et al., 2003, fig. 1) and *Tuarangisaurus* (in which the process is somewhat longer in *T. keyesi* than in QMF11050). The retroarticular process is rather long in *Thalassomedon* (Carpenter, 1999, fig. 12), *Libonectes* (Carpenter, 1997, fig. 5), *Hydrotherosaurus* (Welles, 1943, fig. 4) and *Brancaesaurus* (GPIM A36, Sachs, pers. obs. 1999).

16. Axis shape. *0*. centrum short and high. *1*. centrum long and low. (modified from Carpenter, 1999). Outgroup. The axis is short and high in *Muraenosaurus* (Andrews, 1910, fig. 49). Ingroup. The axis centrum is short and high in *Brancaesaurus* (Wegner, 1914, fig. 2), *Libonectes* (Carpenter, 1997, fig. 1), *Thalassamedon* (Welles, 1943, plate 22), *Occitanosaurus* (Bardet et al. 1999, plate 2), *Aristonectes* (Cabrera, 1941, fig. 2), *Hydrotherosaurus* (Welles, 1943), *Callawayasaurus* (UCMP38349, Sachs pers. obs., 2001) and *Tuarangisaurus*. The centrum is long and low in *Styxosaurus* (Sachs, 2004), *Hydralmosaurus* (Cope, 1877) and *Elasmosaurus* (Cope, 1869, plate 2). The axis vertebra is unknown *Terminonator* (Sato, 2003).

17. Shape of the cervical centra. *0*. anterior cervical centra shorter than high or the length and height is about equal. *1*. anterior cervical centra longer than high. Outgroup. In *Muraenosaurus* the length and height are about equal (Andrews, 1910). Ingroup. The anterior cervical centra are longer than high in *Styxosaurus* (Sachs, 2004), *Hydralmosaurus* (Cope, 1877), *Libonectes* (Welles, 1949), *Elasmosaurus* (Welles, 1952), *Occitanosaurus* (Bardet et al., 1999), *Callawayasaurus* (Welles, 1962), *Terminonator* (Sato, 2003), *Hydrotherosaurus* (Welles, 1943) and *Tuarangisaurus*. These measurements are about equal in *Thalassomedon* (Welles, 1943), *Brancaesaurus* (Wegner, 1914) and *Aristonectes* (Cabrera, 1941).

18. Cervical vertebrae number. *0*. fewer than 30. *1*. 30–40. *2*. 40–50. *3*. 50–60. *4*. 60 or more. (modified from Carpenter, 1999). Outgroup. *Muraenosaurus* comprises 44 cervicals (Brown, 1981). Ingroup. The number of cervicals is lowest in *Brancaesaurus* (37, Wegner, 1914), *Occitanosaurus* (43, Bardet et al., 1999), *Terminonator* (51, Sato, 2003) and *Callawayasaurus* (56, Welles, 1962). The number of cervicals is 60 or more in *Hydrotherosaurus* (60, Welles, 1943), *Libonectes* (62, Carpenter, 1999), *Thalassomedon* (62, Welles, 1943), *Styxosaurus* (62, Carpenter, 1999), *Hydralmosaurus* (62, Welles, 1999) and *Elasmosaurus* (72, ANSP10081, Sachs pers. obs. 2001). The total number is unknown in *Aristonectes*, but at least 23 cervical vertebrae are present in MLP 40-XI-14-6 (Cabrera, 1941, Gasparini et al., 2003) and *Tuarangisaurus*.

19. Lateral longitudinal crest on cervical centra. *0*. absent. *1*. present. (sensu Bardet et al., 1999). Outgroup. A lateral longitudinal crest is present in *Muraenosaurus* (Andrews, 1910). Ingroup. This character is present in all elasmosaurs except for *Brancaesaurus* (Wegner, 1914), which is a juvenile.

EXPLANATION OF THE PHYLOGENETIC ANALYSIS

METHODS. The data matrix (Table 1) was analysed using PAUP version 3.1.1 (Swofford & Begle, 1993) with 100 heuristic searches and random addition of sequences. The first goal of the analysis was to show an example for the possible interrelationship of the Elasmosauridae; the second goal was to find the position of *Tuarangisaurus* within the family. All characters

were left unordered. With a heuristic search, 3 equally most parsimonious trees were obtained, each with a length of 32 steps, a consistency index (CI) of 0.719, homoplasy index (HI) of 0.281 and retention index (RI) of 0.763. All trees support the position of *Libonectes* as sister taxon of *Thalassomedon*, *Terminonator* as sister taxon of *Aristonectes* and *Styxosaurus* as sister taxon of *Hydralmosaurus*. In all trees *Tuarangisaurus* and *Callawayasaurus* have a single standing position (Fig. 8). The principal difference of the trees is the position of *Callawayasaurus*, which is either the sister taxon of group 7 or of group 8.

Group 1 includes all elasmosaurs, except for *Brancasaurus* where character 19, the longitudinal lateral crest in the cervical centra, is not present. According to Brown (1993) the crest is a diagnostic feature for the Elasmosauridae, but is only fully developed in adults. However, as shown in *Styxosaurus glendowerensis* (Saehs, 2004), a well developed crest can be present in juveniles too. Thus it remains questionable if *Brancasaurus* really represents an elasmosaur or would rather belong in the relationship of the Cryptoelididae (supported by two characters only present in *Brancasaurus* and *Muraenosaurus*; 1(0) and 18(2)).

Group 2 includes the members of groups 4, 7 and 8 based on characters 6(1) and 15(1). The maxilla is primitively more expanded posteriorly than at the level of the last dentary tooth and the retroarticular process is then usually also rather long. Both characters can therefore be quoted as advanced if present. Group 3 includes elasmosaur taxa showing more plesiomorphic conditions, containing the members of group 5 and 6 as well as *Hydrotherosaurus*. It is characterised only by character 15(0), an elongate retroarticular process. Group 4 includes *Callawayasaurus*, *Tuarangisaurus* and group 7, showing a feature complex of characters 5(1) + 8(0) that is unique for this group. Group 5 comprises the most basal members of the Elasmosauridae, thus showing characters 3(0), 7(0), 10(0) and 11(0) as plesiomorphic conditions that are characteristic for this group. Group 6 that is formed by *Thalassomedon* and *Libonectes* is characterised a feature complex of character 6(0) + 18(4) that is unique among the Elasmosauridae.

Group 7 shows a number of advanced features, e.g. character 5(2), 13(2), 16(1) and 18(4) that in this combination is only present in this group. It can be concluded that an elongate but low axis

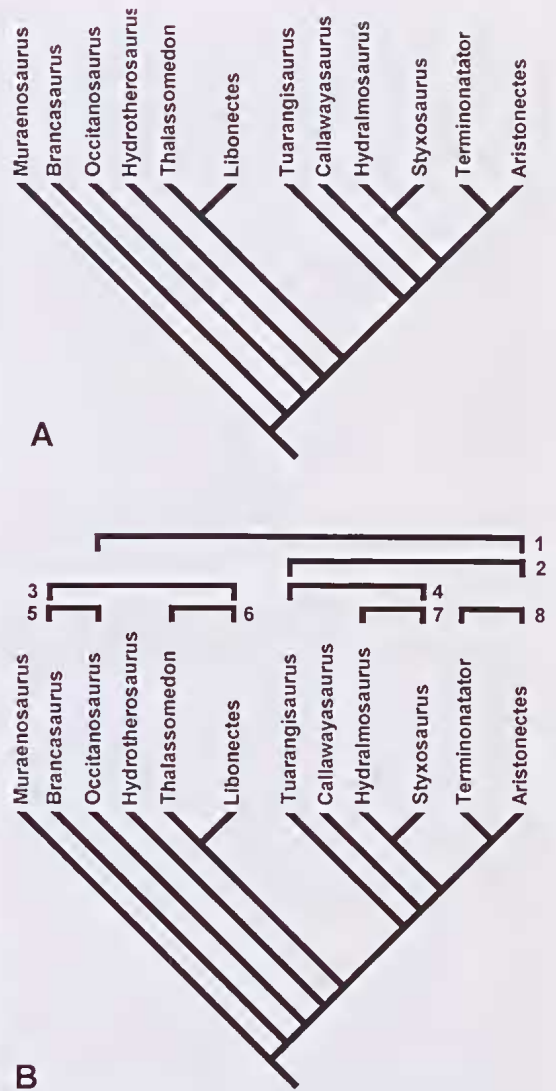


FIG. 8. Phylogenetic tree of the Elasmosauridae. A, consensus tree, showing the position of *Tuarangisaurus* and its interrelationships; B, composition of groups 1-8.

centrum is an advanced feature, especially considering the fact that the number of cervical vertebrae is equal with that in *Libonectes* and *Thalassomedon* where a more quadratic shaped axis centrum is developed. These characters support the high phylogenetic position of group 7. Considering the fact that an elongate and low axis centrum, together with the most increased number of cervical vertebrae in all sauropterygians is also present in *Elasmosaurus platynurus*, it can be concluded that this taxon probably belongs to

TABLE 1. Data matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
<i>Muraenosaurus</i>	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	1	
<i>Ocitanosaurus</i>	1	0	0	0	2	?	0	0	0	0	0	?	?	?	0	1	2	1		
<i>Brancasaurus</i>	0	0	0	2	?	0	0	1	1	0	0	0	0	0	0	0	1	0		
<i>Libonectes</i>	1	0	1	1	1	0	1	1	1	1	1	?	1	1	0	0	1	4	1	
<i>Thalassomedon</i>	1	1	1	2	2	0	1	1	1	1	1	1	1	0	0	0	0	4	1	
<i>Tuarangisaurus</i>	1	0	1	1	1	1	1	0	1	1	1	1	0+1	1	1	0	1	?	1	
<i>Callawayasaurus</i>	1	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	1	3	1	
<i>Styxosaurus</i>	1	0	1	1	2	1	1	0	1	1	1	1	2	1	1	1	1	4	1	
<i>Hydralmosaurus</i>	1	0	1	1	2	1	1	0	1	1	1	0	2	1	1	1	1	4	1	
<i>Aristonectes</i>	?	2	?	?	0	1	?	?	?	?	?	?	0	1	1	0	0	?	1	
<i>Hydrotherosaurus</i>	1	0	0	?	2	?	?	?	1	?	1	0	?	1	0	0	1	4	1	
<i>Terminonator</i>	?	2	1	2	2	1	?	?	1	?	1	?	?	1	1	1	?	1	3	1

group 7 too. Group 8 is characterised by only one character 2(2), the incisement of premaxillary teeth.

DISCUSSION. This analysis indicates that *Tuarangisaurus*, is more primitive than *Styxosaurus* and *Hydralmosaurus* from the Western Interior Seaway of North America, *Terminonator* from the Maastrichtian of Canada and *Aristonectes* from the Maastrichtian of Patagonia. *Tuarangisaurus* shows characters 3(1), 6(1), 12(1), 14(1), 15(1) and 17(1) as advanced features. It is more advanced than group 3 in characters 6(1) and 15(1); more advanced than group 5 in characters 3(1), 6(1), 7(1) and 10-15(1); more advanced than group 6 in characters 6(1) and 15(1) and more advanced than *Hydrotherosaurus* in characters 3(1), 12(1) and 15(1). *Tuarangisaurus* is less advanced than *Callawayasaurus* in character 5(2), less advanced than group 7 in characters 5(2), 13(2) and 16(1) and less advanced than group 8 in characters 2(2) and 4(2). Thus *Tuarangisaurus* belongs in the closer relationship of group 7 and *Callawayasaurus*, but seems to be less advanced than both.

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TABLE 2. Measurements of the alveols (approximate), skull and postcranial elements.

Pmt 1	?mm	Dt 1	11mm	Length of the skull anteroposteriorly	40cm
Pmt 2	?mm	Dt 2	16mm	Anteroposterior length of the premaxilla along the alveolar-part	ca. 7.0cm
Pmt 3	?mm	Dt 3	15mm	Anteroposterior length of the maxilla	ca. 2.1cm
Pmt 4	12mm	Dt 4	14mm	Height of the maxilla at the anterior edge of the orbita	ca. 6.0cm
Pmt 5	13mm	Dt 5	12mm	Length of the posterior process of the maxilla	ca. 6.0cm
Mxt 1	8mm	Dt 6	11mm	Largest distance between the posterior edge of the external naris and the anterior edge of the orbita	1.7cm
Mxt 2	12mm	Dt 7	9mm		
Mxt 3	13mm	Dt 8	?mm	Anteroposterior diameter of the external naris	2.3cm
Mxt 4	13mm	Dt 9	10mm	Dorsoventral diameter of the external naris	1.2cm
Mxt 5	11mm	Dt 10	10mm	Anteroposterior diameter of the orbita	8.0cm
Mxt 6	8mm	Dt 11	9mm	Length of the jugal anteroposteriorly	ca. 8.0cm
Mxt 7	8mm	Dt 12	13mm	Length of the mandibular symphysis	6.2cm
Mxt 8	7mm	Dt 13	12mm	Length quadrate condyle	3.6cm
Mxt 9	7mm	Dt 14	11mm	Breadth quadrate condyle	1.4cm
Mxt 10	6mm	Dt 15	10mm	Height quadrate condyle	1.4cm
Mxt 11	?mm	Dt 16	9mm	Length of the hyoid anteroposteriorly	10.0cm
Mxt 12	?mm	Dt 17	9mm	Breadth of the hyoid posteriorly	1.0cm
Mxt 13	?mm	Dt 18	7mm	Height of atlas-axis complex	3.4cm
Mxt 14	?mm			Breadth of atlas-axis complex	3.3cm
Mxt 15	?mm			Length of anterior cervical vertebra	6.4cm
				Breadth of anterior cervical vertebra	6.9cm
				Height of anterior cervical vertebra	5.0cm
				Length of first posterior cervical vertebra	9.8cm
				Breadth of first posterior cervical vertebra	10.4cm
				Height of first posterior cervical vertebra	8.3cm

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